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SOIL REMOVED BY VOLES OF THE GENUS PITYMYS IN THE SPANISH PYRENEES[1]

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ABSTRACT.- The erosiogenic activity of Pyrenean mountain voles is studied following the measures taken in an experimental plot in the Western Pyrenees. An easy model for estimating the volume and weight of soil carried to the surface by voles is presented and used to quantify this amount in natural conditions. Fossorial Pyrenean rodents seem to dislodge well over 6 Tm/ha.yr of soil on the colonized areas above the timberline. The four stages (new, recent, old, and vegetated) of the evolution of soil heaps are discussed. Finally, an attempt is made to evaluate the rate of horizontal sediment transport due to the direct action of voles, with a maximum result of 17 cm³/cm.yr, quite comparable to pure geoclimatic rates.

RESUMEN.- Se estudia la actividad de movimiento del suelo de los roedores pirenaicos del género Pitymys, *a partir de los datos obtenidos en una parcela experimental situada en los Pirineos Occidentales. Se presenta un modelo sencillo para estimar la cantidad de tierra removida a partir de medidas que pueden tomarse fácilmente en el campo, y se emplea dicho modelo para evaluar esta magnitud en condiciones naturales. Al parecer, los roedores subterráneos pueden sacar al exterior más de 6 Tm de tierra por hectárea y año en las zonas epiforestales que colonizan. También se discute la evolución del suelo removido y sus condiciones para la erosión por escorrentía. Finalmente se intenta evaluar la tasa de transporte horizontal del sedimento debida a los animales, que resulta ser de hasta 17 cm³ por cm y año, un valor claramente comparable con los debidos a agentes geoclimáticos.*

RESUME.- On a étudié l'activité fouisseuse des campagnols pyrénéens du genre Pitymys, *d'après les données recueillies dans une enclosure experimentelle située dans les Pyrenées de l'Ouest. On presente un modèle simple permettant d'estimer la quantité de sol mue par les campagnols a partir de mésurements qu'on peut prendre avec facilité sur place, et on emploie ce modèle sur les données prises dans la nature. Il en résulte que les rogeurs souterrains peuvent extraire bien plus de 6 tonnes de terre para hectare et*

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année dans les zones de montagne qu'ils colonisent. On discute aussi l'évolution du sol porté à l'exterieur, ses conditions pour etre emporté par la pluie et le taux de transport horizontal de sédiment du à l'activité des animaux. Le résultat, jusqu'à 17 cm³ par cm et année, est bien comparable avec ce qui résulte de l'action des agents climatiques.

Key words: *Fossorial rodents, Bioturbation, Pyrenees, Erosion, Transport rate.*

The study of the habits of fossorial mammals in mountain ranges is essential in any attempt to understand the functioning of mountain ecosystems, because these animals are one of the main factors affecting the soil loss in some mountain areas. High mountain fossorial mammals, because of their erosiogenic activity, have been studied in several mountain chains in the Northern Hemisphere, such as the Alps (LE LOUARN, 1977), the Rockies (ELLISON, 1946), or the Pamir (ZIMINA & ZLOTIN, 1980). We can find some data for the French Pyrennes in HIPPOLYTE (1987) and DENDALETCHE *et al.* (1985), but for the Spanish Pyrenees there are only preliminary data supplied by MARTINEZ RICA & PARDO (1990).

One of the main problems in the study of bioturbation by mammals is estimating the amount of removed soil with sufficient accuracy. This is often unfeasible, but at least it is possible to evaluate the amount of soil carried up to the surface, because voles, like other fossorial mammals, pile up the earth around the entrance holes, building the well-known earthmounds. The purpose of this paper is, therefore, to quantify the amount of soil piled up on the surface by mountain voles of the genus *Pitymys* above the forest line, and to design a fast method of measuring it in the field.

1. Material and methods

The selected study area is located in the Central Spanish Pyrenees, about 30 km from the town of Jaca, next to the Lecherines peaks, at an altitude of 2000 masl, and hence above the tree-line. The observations were done in an experimental plot of 100 x 100 m, with moderate slope and a grass cover of *Festuca rubra, Trifolium alpinum* and *Nardus stricta.* The area, which is grazed by cattle and is fairly frequented by people, is nevertheless, densely populated by the mentioned vole species and by other animals.

The plot was subdivided into one hundred smaller squares of 10 x 10 m; each square was monitored during the active season, the number of earthmounds were counted and their condition registered. For each earthmound height and diameter were measured, and the relative age (new, recent or old) noted. Other features of the biotope were registered: soil depth, slope, plant cover, quantity of stones and rock outcrops, and mean diameter of the stones were noted for each square. Moreover, 130 earthmounds were carried to the laboratory and their fresh and dry volumes and weights were taken. When needed, the soil was dried in a stove during 48 hours, at 100 °C.

Five species of burrowing voles inhabit the upper levels of the Central Pyrenees, and four of these, *Pitymys pyrenaicus, P. duodecimcostatus, P. lusitanicus* and *Microtus arvalis* live in the observation area. Only those of genus *Pitymys* were studied, because these are true fossorial species; *Microtus arvalis* does not dig very much in that place. However, as the differentiation of these species is very hard in the field (even when captured), we have treated all them as only one set "mountain voles".

2. Results

1. The regressive model

Earthmound weight and volume depend, of course, on the corresponding height and diameter, but the relation is not strict as other factors, such as soil density or mound age play some part. Fresh weight, for instance, is mainly affected by the water content of the soil; a standard measure, allowing comparison with the results of other authors, is needed, and probably the best would be the volume of well-dried and packed soil, but as this is not easy to measure on the field, we have tried different ways (GIANNONI *et al.*, in prep).

TABLE 1

The regressive model of mound dry weight and volume estimation

PARAMETER	VALUE $(WEIGHT)^{1/3}$	VALUE $(VOLUME)^{1/3}$
Constant	1.611	1.480
Diameter Coeff.	0.255	0.250
Height Coeff.	0.200	0.321
Determ. Coeff.(R)	0.873	0.966
t Value Const.	7.211	8.604
t Value Height	5.138	7.267
t Value Diam.	14.290	12.929
Standard Error	0.911	0.568
Model Mean Square	369.072	238.780
Error Mean Square	0.830	0.323
F	444.442	739.19
N	130.	53.

All values are significant at 99.99% level

In the sample of dried mounds, 130 diameter and height measurements were taken. Mean diameter was 18.6 cm and mean height 7.4 cm.

Real volume of the mounds was measured on a graduated beaker, and the mean in a sample of 53 observations was 574.3 cm^3. Trying different geometrical models with the given height and diameter, we arrive at volumes ranging from 670 to about 1800 cm^3. The use of a geometrical model to estimate volume of soil heaps is not, therefore, very accurate.

For that reason we tried an empirical model based on the regression of the volume on height and diameter of the mounds. Raw volume or weihgt were not regressed directly on the data; instead, to linearize the relationship, the cubic root of both variables was used. The results, first published in the paper by GIANNONI *et al.* (in press) are given here in the Table 1; see also Figs. 1 and 2.

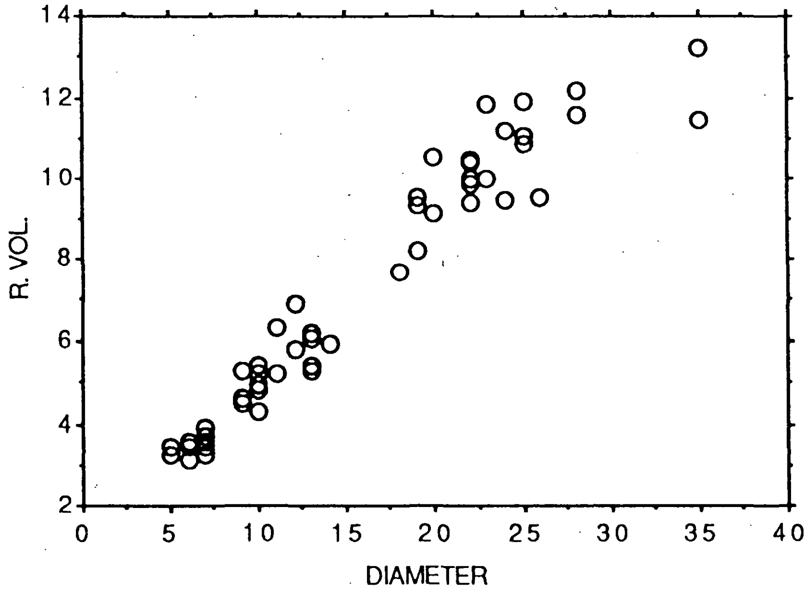

Fig. 1: Projection of the multiple regression model on the plane defined by the independent variable and diameter.

The best correlation to be found is between the cubic root of volume and the diameter ($R^2 = 0.933$, $p \ll 0.0001$). Correlation with height is not so strong ($R^2 = 0.86$), and like the first one, is due to a general size factor. When the contribution of the first variable is controlled, correlation between volume and diameter decreases ($R^2 = 0.51$) but still remains significant ($p < 0.001$). The volume of a mound thus depends on the corresponding diameter, and to a lesser degree, on the corresponding height.

Correlations between fresh or dry weight and the dimensions of mounds are weaker, but also clear. In both cases diameter seems to be more closely correlated to weight ($R^2 = 0.85$) than to height ($R^2 = 0.67$ and 0.68). This is probably due to the variable density of soil.

Using this model to compute the volumes from the measured dimensions, we arrive at a mean heap-volume of 597.6 cm^3, which is not very different from that obtained from direct measurement. Thus, we can deduce that our regression model is sufficiently reliable, and that the volume of earthmounds can be accurately guessed from height and diameter measurements easily taken in the field.

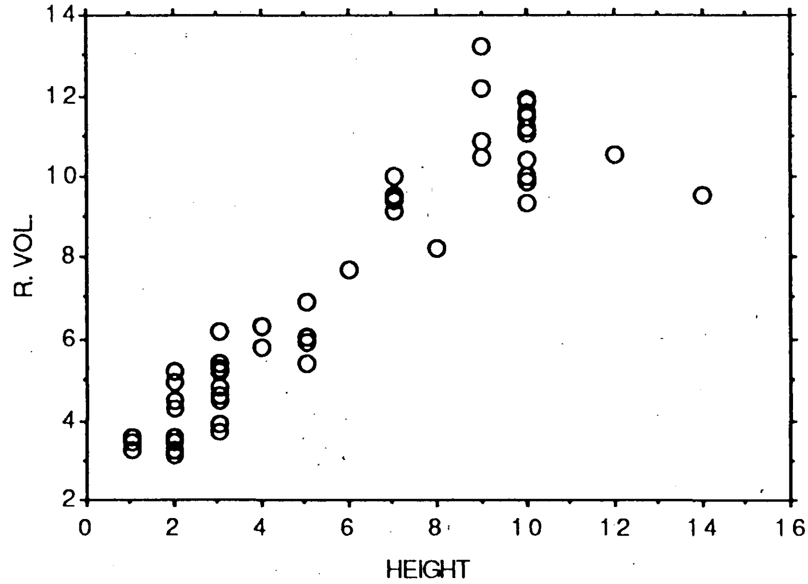

Fig. 2: Projection of the multiple regression model on the plane defined by the independent variable and the height.

As we have already said, we have tried different geometric models, such as the spheric dome, the cone, the parabolic dome and even the cylinder. The estimated volume (or better, its cubic root) has been compared in each case to the corresponding measured value, and the difference has been noted. The average difference was 1.93 for the cylindric model, 0.97 for spherical dome, 0.88 for the paraboloid, 0.65 for the cone and 0.28 for the regressive model. Thus, this last model seems again to be more accurate than the others.

2. *Removed soil in the field*

After building the model we are in a position to estimate the volume of the earthmounds in the field. Within our observation plot the number of mounds was 1060, with a mean diameter of 16.4 cm and a mean height of 6.31 cm.

Thus, the mean surface covered by an earthmound is 211.2 cm^2, and the surface covered in the entire plot, 22.4 m^2 (i.e. 0.2% of the plot area). Of course, there are zones without removed soil, while others have up to a 4% of their surface covered by mounds. As stonier areas are hardly colonized by voles at all, it is clear that the areas with best soil are those having a higher percentage of the surface covered.

From the given measurements of mean diameter and height we can estimate the mean volume of an earthmound at 438 cm^3. However, we have estimated independently the 1060 volumes from the measurements of each mound. Frequency distribution of mound size is shown in Fig. 3. The mode is located between 400 and 800 cm^3; distribution is clearly skewed, and the larger mounds are, thus, poorly represented in the sample.

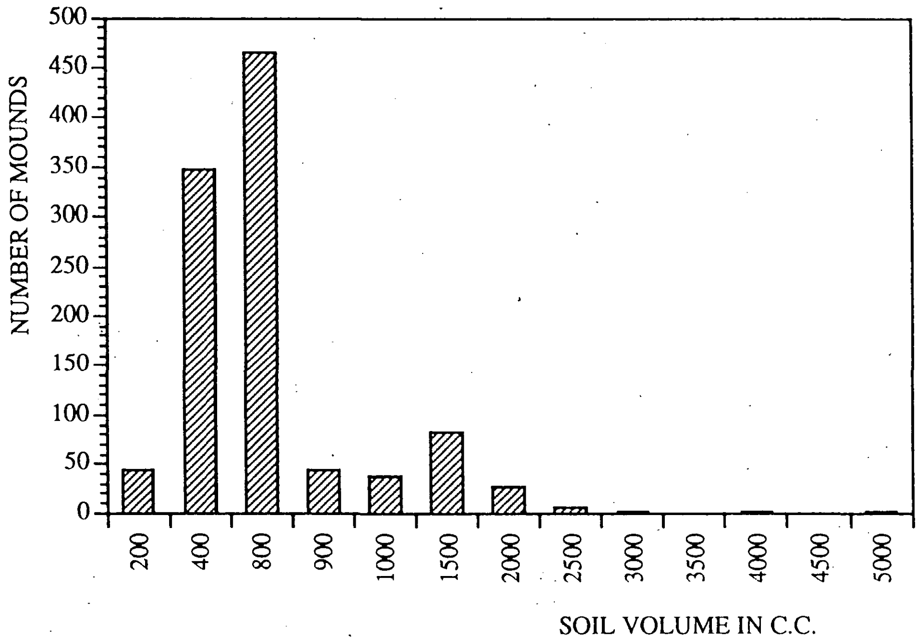

Fig. 3: Frequency distribution of mound size.

The resulting average volume is 585 cm^3, with extreme values of 105 and 4581 cm^3. Thus, the total volume of soil brough to the surface in the plot was 0.62 m^3. The mean fresh soil density being 0.8 g/cm^3, this means a weight of roughly 500 kg/ha. If we restrict our estimation to new earthmounds, 24 hours old at most, mean volume for the whole plot is 60425 cm^3.

This value is lower than most of those given for other rodents. Nevertheless, many of the data found in the literature refer to a period of one year, while our estimate was made from observations taken over four months. Moreover, we have counted only new, or new and recent mounds, which are rarely over one day, or one week old. Thus, to obtain an estimation of the soil removed during a year, we must multiply our value by a quite high number. Let us take a very conservative position, and hence discard all the burrowing activity which took place out of the active season; we know that this is excessive, because there is intense activity during the winter, and the weight of the soil cores laid down on the surface after the snow melting is not negligeable (HIPPOLYTE, 1987); but let us reduce the activity time to the peak months of the mountain summer (in the Pyrenees, from June to September). Let us also to give a mean age of 48 hours to the new mounds, although this is a very large estimation. Thus we should multiply our by 61, and therefore, an estimate of the weight of soil carried to the surface by fossorial voles is, in our plot, at least 3.69 $m^3.ha^{-1}.yr^{-1}$, that is, about 2.9 Tm. $ha^{-1}.yr^{-1}$, if we count only new mounds to avoid the age estimation problems.

Although our estimation is far more reliable than most of those given in literature, there are some points which deserve comment. Restricting the count to new mounds allows a more accurate age estimation. Other innaccuracies are unavoidable, but all of them point towards a larger amount of removed soil. The average age of the mounds, for instance, may have been overestimated, and soil removal under the surface is not recorded at all. What's more, condensing the whole year's activity into four months is only a guess.

For all these reasons, our results may show a very low estimation; we may say, to summarise, that the amount of soil carried to the surface by voles, above the tree level in the Pyrenees, definitely surpasses 6 and probably 10 $Tm.ha^{-1}.yr^{-1}$; of course, this value applies only to areas inhabited by voles.

3. *Evolution of removed soil*

Rodent soil dislodging has several consequences for the biotope, both under and above the surface. Let us look only at the changes in the soil carried outwards, and specially at the evolution of earthmounds.

The earth which has just been carried to the surface contains humidity and is, therefore, dark. Water evaporates rapidly, depending on the air temperature and humidity. If there is no rain, the change takes place in a few hours even when air humidity is high and temperaturre low. Mounds showing these features have been counted as new (N), and form a small percentage (10%) of the total. Maximum age of new mounds has been estimated at 24 h. The corresponding low proportion is therefore normal.

When the outer layer of a mound is already dry, but earth is still loose, and grains are not yet glued together, the mounds are called recent (R). The duration of this stage depends also on climatological factors, mainly on rainfall. Rain causes a water suspension of fine particles in the outer mound layers, and when dried and evaporated, the suspension glues together the larger particles. Moreover, the impact of raindrops often causes a further compactation of the soil. The mound loses its texture and becomes smaller. Of course, if rain comes just after the earth is carried outwards by the voles, quite new mounds may become old, whereas if there are a number of days without rain, the age of a recent mound may be higher.

In our plot, about 30% of the counted mounds were recent; if we accept a maximum age of 24 h for new mounds, this might mean that the maximum age of new mounds would be, on average, about three days. In fact this age is highly variable and cannot be stated so clearly; as a conservative estimate, we have taken one week, but this value is probably too high.

After the compacting of outer layers, mounds enter the third stage of their evolution, and become old (O). Old earthmounds in our plot make up the remaining 60%. This may mean that their age does not surpass three weeks, but this is still more variable than for the earlier stages. Tagged mounds in some places were completely covered by plants, and were undistinguishable after about two months, while others, especially those built just before the winter, may remain for several months, or even one year. The end of the old stage is marked by the beginning of plant recolonization, or when all the soil is washed away, leaving only a hole within a bare patch (this case is less frequent). An average duration of one month is a prudent guess; older mounds begin to show the new plants sprouts because, during the rainy season, the first rain starts the germination of the seeds or buds contained within the soil. Summer and fall mounds, however, last longer in the old stage, because the lack of seeds or water.

Recolonization by plants is the last phase of the mound evolution, and afterwards the only indication of the previous presence of earthmounds is the mammillate microtopography of the recolonized areas. Grass roots keep the soil in place, and erosive losses cease. Erosion processes in the mounds therefore, only last, while the soil remains exposed, i.e. for a short time, but this time is also that of maximum rainfall, and soil may be washed away in large amounts, although most of it remains in place. The finest particles are the first ones to be washed away, and therefore, one of the consequences of the aging of earthmounds is a change in granulometry. Stabilization of the mounds also follows from the coarsening of surface, which is a consequence of the granulometric change.

The amount of mound soil carried away by runoff is small. Decrease in volume is less than 25% for *Thomomys bottae* (BLACK & MONTGOMERY, 1991), and probably, less than half this volume represents material transported downslope (IMESON & KWAAD, 1976).

More detailed data on the evolution of dislodged soil are being gathered now, in particular on the plant colonization phase is studied, and the comparison of different colonization strategies. The monitoring of changes in plant composition, nutrient contents of the soil, and soil structure is on the way.

3. Discussion

The part played by rodents in mountain soil formation and movement is well known (SMITH & GARDNER, 1985), but most of the papers deal with the amount of removed soil, and few give indications about the importance of animals in erosive processes. Recently BLACK & MONTGOMERY (1991) have tried to quantify the importance of the horizontal transport of sediments by Californian geomyids; according to them, the importance of the voles on *direct* horizontal transport is one order of magnitude smaller than that of abiotic processes. Of course, the main contribution of animals to sediment transport is indirect, and takes place by interaction with abiotic processes.

The referred authors estimate the importance of direct transport processes by means of RAPP (1960) formula, which relates the rate of transport to the volume of sediment, the transport distance, the area of the studied plot and the considered time. If we try to apply the formula to our data, first of all we need to know these variables.

The plot area is, of course, the easiest value to obtain. Our plot has an extension of 1 ha, which is about twice the size of the cited authors' plot. The volume of removed soil has been already estimated at a minimum of 3.69 m^3, and the time span of observation was four months although we have given estimate as corresponding to the whole year. The only remaining value needed is the average distance covered by dislodged soil.

BLACK & MONTGOMERY (1991) use three methods to bracket the average covered distance, all of them rather inaccurate. In fact these methods provide only the minimum, intermediate and maximum transport distance, and the authors guess the probable average distance from these values. Here, we apply their methods, with some improvements, to the data of voles, with the following results:

Minimum distance covered by sediment equals the diameter of the earthmound. BLACK & MONTGOMERY (1991) say that this is a minimum estimate when the entrance hole is on the upper border of the mound, but we find that unrealistic, and have discarded the procedure. We take as a minumum their intermediate estimation, that is, the distance between the centroid of the earthmound and the centroid of the adjoining upwards tunnel. These distances are being measured directly, and we do not have the data yet, but we can estimate the result from initial guesses. The centroid of the tunnel is easily found by means of geometry (see Appendix), although this is perhaps innecesary, given the scarcity and roughness of the available data. To do this we need the average lenght and inclination of the upwards tunnel, which we deduce in the appendix, and from which a minimum horizontal transport of 17 cm for each mound results, if a mean inclination of 60° and a mean lenght of 46 cm is accepted for the upwards burrow.

The maximum distance is obtained from the spatial distribution of earthmounds, which, of course, is neither random nor regular. According to this hypothesis, the mound soil not only comes from upwards tunnels but also from the subhorizontal burrows connecting these ascending branches, and therefore, maximum transport distance is half the average distance between holes. To be conservative, let us suppose that each hole is only connected to its closest neighbour, thus making the mean distance lowest. The expected average distance between nearest neighbours in a random spatial pattern has been known since the classic paper by CLARK & EVANS (1954), and equals the inverse of the square root of the mean density. In the present case, with a mean density of 0.106 mounds/m^2, the corresponding value is 3.07 m, and half this distance, 153 cm, is the maximum horizontal transport lenght.

We are now in a position to estimate the mean transport rate. Of course, given the large difference between the minimum and the maximum transport distance, corresponding rates will differ widely, but these are the best estimations available until direct measurement finishes. Applying RAPP formula we have:

$$R_{min} = \frac{3690000 \times 17}{108 \times 0.3333} = 1.88\ cm^3.cm^{-1}.yr^{-1}$$

for the minimum rate, and:

$$R_{max} = \frac{3690000 \times 153}{108 \times 0.3333} = 16.94\ cm^3.cm^{-1}.yr^{-1}$$

The rates obtained are much higher than those given by BLACK & MONTGOMERY (0.48 to 5.88 $cm^3.cm^{-1}.yr^{-1}$). But this difference is probably due to direct application of the formula. The value of 0.3333 yr (four months) in the denominator might be justified if burrowing activity were constant and intense throughout the year; in fact, a decrease in this activity would mean a higher time span value, and a lower rate. Also the fact that spatial distribution was taken as if at random, when in fact it is highly clustered, means an overestimation of the rate, True values are probalby half those given here, but in any case, well within the range of those found for other species. We must await direct measures to settle the question.

The main purpose of this paper is to supply data on the importance of erosive processes carried out by fossorial rodents in the Spanish Pyrenees. Although there are already some published data on the subject (MARTINEZ RICA & PARDO, 1990; MARTINEZ RICA *et al.,* 1991), these were preliminary, and results become more and more accurate as the study progresses. Those in the present paper are quite reliable, and show us that rodents must account for a large part of the soil movement and loss above the three-line in Mediterranean mountains. While we have clear indications as to the volume of removed soil, and these compare well to those supplied by other authors, estimations of real erosion, that is the washing away of dislodged soil, are not so accurate, and must be still considered preliminary. However, they are also comparable to the few bibliographic data.

It is clear anyway, that the main contribution of fossorial animals to mountain soil changes is indirect, and estimations of that are simply not yet available. We have no more data on the other important part played by animals in the structuring of mountain soil. After the formation of mountain regolith, animals are the main source of heterogeneity available, and therefore it is worth continuing the study of the different actions which are due to them, and try to answer the many questions still open on the subject.

Acknowledgements

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Appendix

Previous papers assimilate the soil heaps to hemispherical mounds, with the center located at one radius from the entrance note. We have attempted a more accurate model as follows (see Figs. 4 and 5):

The centroid of the upwards tunnel is easy to locate if we assimilate this tunnel to a cylinder, running downwards from the hole to the point where it changes direction. The average length of the cylinder can be found if we consider the mound soil packed within the tunnel, and take the average diameter as 4 cm, the average body width of the voles. A cylinder with a volume of 585 cm^3 and a diameter of 4 cm must have a length of over 46 cm. The position of the centroid depends mainly on the shaft inclination, which we have taken as 60° on average. Vertical lenght of the tunnel is, thus, 46° sin60, and horizontal lenght 46° cos60. The centroid lies, therefore, about 11.5 cm away from the entrance hole, and about 20 cm down it.

The centroid of the soil heap is more difficult to locate. To assimilate the mound form to a hemisphere is, as we have seen, incorrect, whereas a spherical dome or calotte is more accurate, the height (b) of the mound being, in effect, smaller than the radius (a/2). Given the equation of a circumference of radius r (different from a/2, the radius of the mound base),

$$\frac{x^2}{r^2} + \frac{y^2}{r^2} = 1$$

we may integrate the function to find the area in the following way:

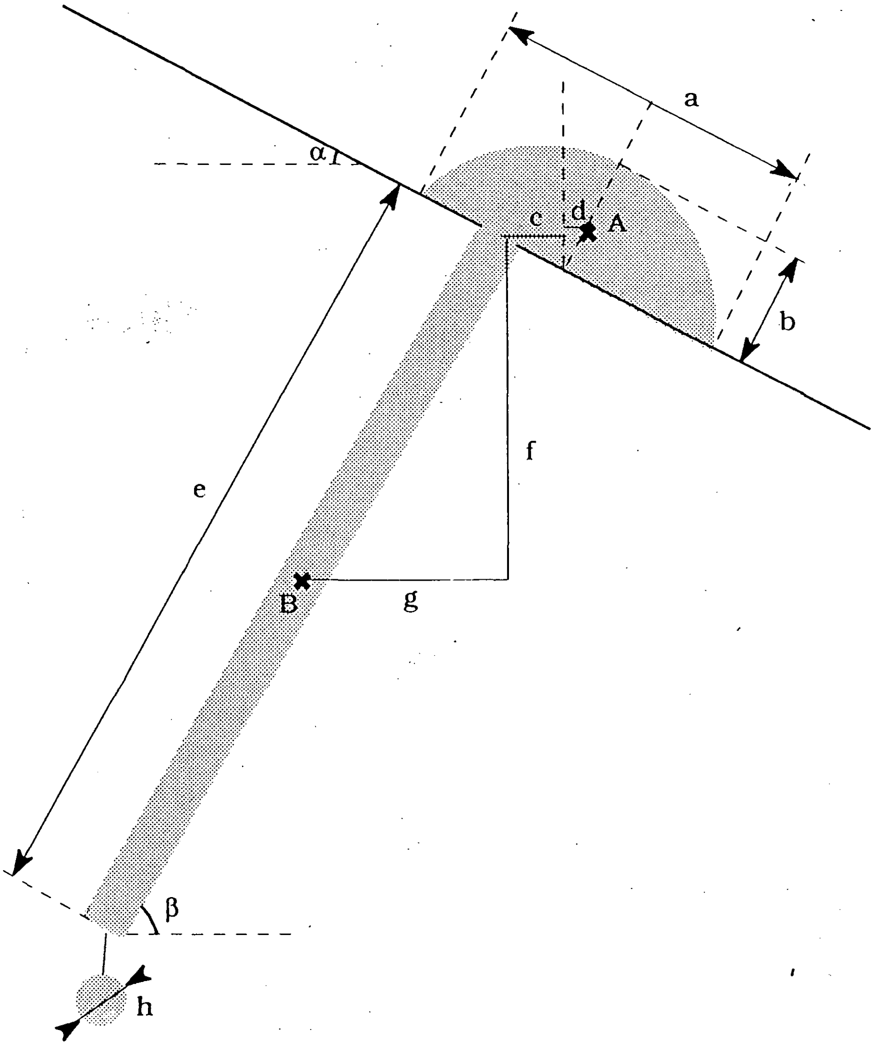

Fig. 4: A sketch of the soil moved by a vole to build a mound. The form, a spherical dome, is idealized, and the measures are the average of those taken. A: Centroid of the mound; B: Centroid of the upwards tunnel; a: Diameter of mound (18.4 cm); b: Height of mound (6.31 cm); c:Distance between hole and vertical axis (4 cm); d: Horizontal displacement of the mound's centroid, depending on the slope (1.5 cm); e: Tunnel lenght (46 cm); f: Vertical displacement of soil within the tunnel (17 cm); g: Horizontal displacement of soil within the tunnel (11.5 cm); h: Tunnel diameter (4 cm); α Slope (30°); ß (B: Tunnel inclination (60°).

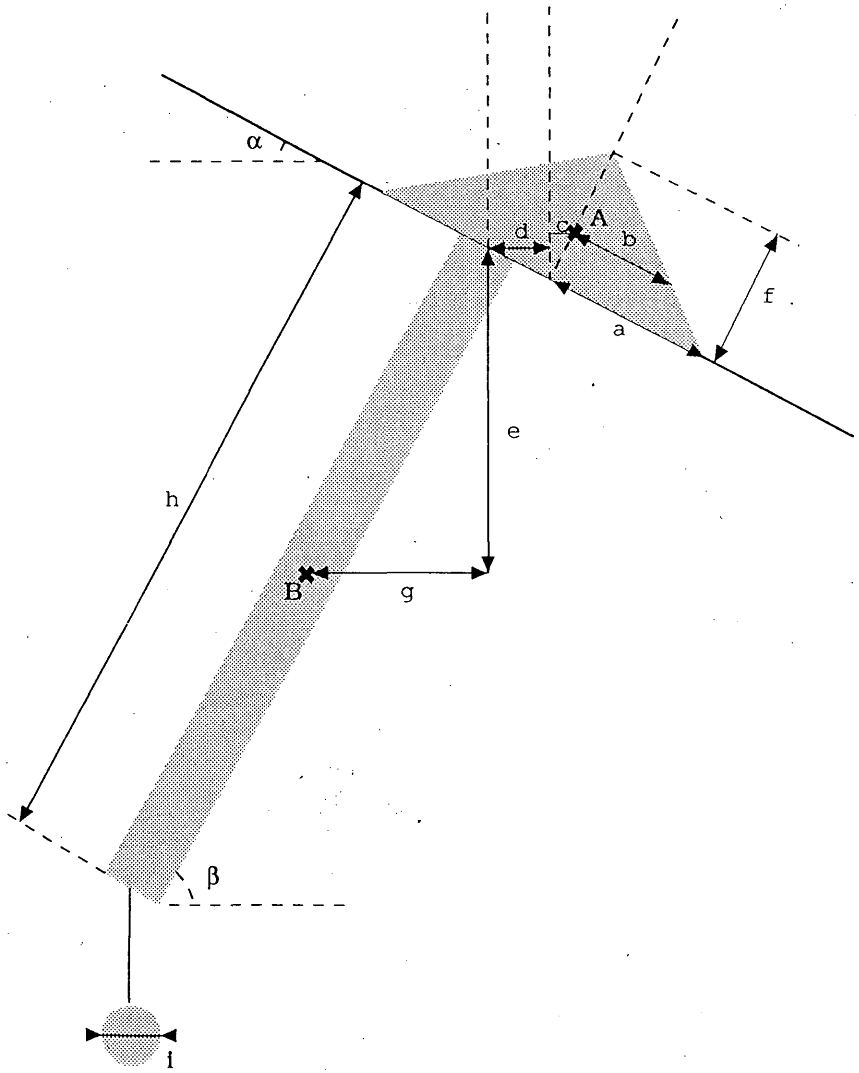

Fig. 5: Same indications as in Fig. 4, but now the heap form is assimilated to a cone. A: Centroid of the cone; B: Centroid of the upwards tunnel; a: Radius of the cone (9.2 cm); b: Radius of the upper cone, having half the volume of the former (7.3 cm); c: Distance between cone centroid an vertical axis, depending on the slope (2.1 cm); d: Distance between hole and vertical axis (4 cm); e: Vertical soil displacement within the tunnel (17 cm); f: Height of the mound (6.31 cm); g: Horizontal soil displacement within the tunnel (11.5 cm); h: Length of tunnel (46 cm); i: Tunnel diameter (4 cm); α Slope; ß: (B: Tunnel inclination (60°).

$$\int_0^b (r^2-b^2)\,dx = \frac{r^2 \operatorname{asin}(b/r)}{2} + \frac{b(r^2-b^2)}{2}$$

The first moment of the area about an axis contained in the mound base is

$$\int_0^b x\,(r^2-b^2)\,dx = \frac{r^3}{3} - \frac{(r^2-b^2)3/2}{3}$$

We are only interested in the vertical centroid coordinate, the horizontal one lying obviously on the symmetry axis of the dome. The preceding calculation would, thus, suffice. First moment divided by area gives the coordinate, which is, therefore:

$$c = \frac{2(r^3 - (r^2-b^2)3/2)}{3\,(r^2 \operatorname{asin}(b/r) + b\,(r^2-b^2))}$$

The radius of the sphere to which the dome belongs can be calculated from the height and the basal radius as

$$r = \frac{((2(a/2)^2-b) + b)^{1/2}}{2}$$

Taking our average values, $r = 8.01$ cm, and $c = 787.6/268.0 = 2.94$ cm.

The centroid of the heap is, therefore, on average, about 3 cm above the surface. Distance from the central vertical line depends, of course, on surface slope; if α is that slope, the distance is easily calculated a 2.94 sin α. For most moderate slopes (α below 30°) that distance does not surpass 1.5 cm.

If we assimilate the mounds to cones, which is more accurate, the estimation of the centroid position is easier. Given the mean height and radius of the mounds, the slope angle of their outer layer is arctan (f/a), that is, 34.45°. The centroid will be located where the volume of the upper part of the cone equals that of the lower part. Height of this upper cone is tan 35.45 times the lenght of the corresponding basal radius (b). Thus, the volume of upper cone must be the half of total volume. That is

$$\frac{\pi b^2}{3}\,0.686b = \frac{\pi a^2}{3}\,h$$

Hence, $b^3 = 389.27$, $b = 7.3$ and the height of the upper cone is 5 cm. The centroid lies, then about 4.2 cm above the soil, and the distance from the central vertical axis does not depass 2.1 cm for slopes under 30°.

We must still add the distance from the hole to the vertical line. This is about 4 cm on the average, and thus we may add all the results to get the average horizontal transport distance as follows:

Transport on the tunnel:	11.5 cm
Distance hole-center vertical:	4 cm
Displacement from center vertical:	1.5-2.1 cm
Total distance	17 - 17.6 cm

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